

A REVIEW OF THE CYCLOSTOMICERATID NAUTILOIDS, INCLUDING NEW TAXA FROM THE LOWER ORDOVICIAN OF ÖLAND, SWEDEN

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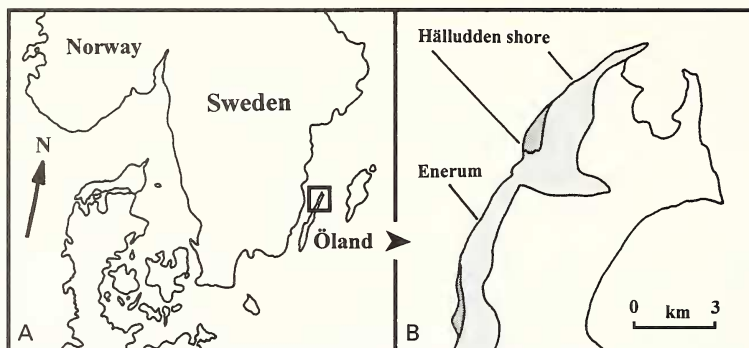
ABSTRACT. Cyclostomiceratidae is a distinct family of early Ordovician, small, gomphoceroid to breviconic ellesmerocerid nautiloids which possess an adorally contracting aperture. The family ranges in age from Arenig to early Llanvirn and is recorded from the USA, northern Argentina, east China and Baltoscandia. This paper reviews the family's status, origin, stratigraphical occurrence and systematics. Three new taxa are described from the lower Kundan Stage of northern Öland, Sweden: *Pictetoceras oliviae* sp. nov., *Parcyclostomiceras paucitimidum* sp. nov. and *Microstomiceras holmi* gen. et sp. nov. These cyclostomiceratids are extremely well preserved and extend our knowledge of the morphology, biostratigraphy and palaeogeographical distribution of the family. *Microstomiceras* gen. nov. is one of the smallest nautiloids described from the Lower Palaeozoic.

ELLESMERO CERID nautiloids are some of the oldest Lower Palaeozoic cephalopods. They evolved from the ancestral plectronocerid nautiloids in China (Anhui and Shaanxi provinces) during the late Cambrian and range into the upper Ordovician where the group is represented by a single family in the Ashgill (Rawtheyan Stage) of Cincinnati (King 1993). Following a brief 'evolutionary explosion' in the late Cambrian when these early cephalopods spread across northern and eastern China, Kazakhstan and central Texas, they underwent a dramatic and sharp decline in terms of both taxonomic diversity and abundance. Three of the four nautiloid orders present in the late Cambrian became extinct before the end of the period, and only a few ellesmerocerid genera survived into the early Ordovician. From these forms, there developed a rich and diverse early Ordovician ellesmerocerid fauna which has been described extensively by Ulrich *et al.* (1943, 1944) and Flower (1964).

When compared with other nautiloid orders, the ellesmerocerids are relatively limited in the form of morphological structures that they developed within their conchs to aid buoyancy regulation. Typically, they exhibit small, narrowly camerate shells with short septal necks and thickened, layered connecting rings. The apical portions of siphuncles of many taxa contain numerous apically directed siphonal diaphragms, although this feature is not exclusive to the group. Diversity amongst the lower Ordovician ellesmerocerids is represented mainly by variations in shell form which are sufficient to provide the basis for systematic classification at family and lower taxonomic levels.

The family Cyclostomiceratidae is a distinctive group of Arenig to lower Llanvirn nautiloids which exhibit typical ellesmerocerid features: they possess small, narrowly camerate conchs with achoanitic to orthochoanitic septal necks and adorally contracting apertures. Siphonal diaphragms have been recorded from at least one taxon (Mutvei and Stumbar 1971). Although the Cyclostomiceratidae has had a varied taxonomic history, the genera currently assigned to the family appear to represent a natural grouping and, following Flower (1964), are presently retained within the order Ellesmerocerida. This assignment is provisional as the cyclostomiceratid muscle scars are of general ventromyarian form (Mutvei and Stumbar 1971; Text-fig. 4A here) which is very different from the dorsomyarian condition known to occur in some other ellesmerocerids (Dewitz 1880). Future classifications may regard this difference as being of high taxonomic significance and, consequently, the order Ellesmerocerida may be divided further.

The study of collections of early Llanvirn cephalopods from the lower Kundan Stage of Öland



TEXT-FIG. 1. A. Geographical location of the island of Öland off south-eastern Sweden. B. Northern Öland and the Ordovician bedrock geology at Hälludden shore and Enerum; the strata are limestones of Latorpian and Volkhovian (dark grey), Kundan (pale grey) and post-Kundan (no ornament) age.

SWEDEN (Öland)	SWEDEN (Öland)	GREAT BRITAIN	GREAT BRITAIN	NORTH AMERICA
STAGES	LIMESTONE FORMATIONS	SERIES	GRAPTOLITE BIOZONE	STAGES
LASNAMÄGIAN	Folkeslunda (part)	LLANVIRN	<i>murchisoni</i>	WHITEROCKIAN
	Seby			
	Skärlov			
ASERIAN	Segerstad		artus	
KUNDAN	Holen			
VOLKHOVIAN	Lanna	ARENIG	<i>hirundo</i>	VALHALLAN
			<i>giberulus</i>	CASSINIAN
LATORPIAN	Latorp		<i>nitidus</i>	
			<i>deflexus</i>	
			<i>(approximatus)</i>	JEFFERSONIAN

TEXT-FIG. 2. Lithostratigraphical and chronostratigraphical nomenclature in Sweden (Öland), compared with British and North American chronostratigraphy and biostratigraphical correlation in relation to graptolite biozones.

(held in the Swedish Museum of Natural History, Naturhistoriska Riksmuseet, Stockholm and the Swedish Geological Survey, Sveriges Geologiska Undersökning, Uppsala) has revealed three new taxa of cyclostomiceratid nautiloids. The specimens, collected by Gerhard and Olivia Holm between 1895 and 1909, come from the lower Holen Limestone Formation (often referred to by Gerhard Holm as the 'grå vaginatumkalk' or grey vaginatum limestone) of Hälludden shore and Enerum,

northern Öland where the formation is superbly exposed in the low-lying cliffs and foreshore (Text-fig. 1). Across this island, strata dip slightly to the east and, with appropriate collecting techniques using distinctive discontinuity surfaces, a high degree of stratigraphical control can be obtained. Further details of the stratigraphy (summarized in Text-fig. 2) are given by Jaanusson and Mutvei (1982).

The Swedish specimens are extremely well preserved and extend our knowledge of the morphology, biostratigraphy and palaeogeographical distribution of the family Cyclostomiceratinae, which has not been recorded from Sweden previously. It is there represented by *Pictetoceras oliviae* sp. nov., *Paracyclostomiceras paucitimidum* sp. nov. and *Microstomiceras holmi* gen. et sp. nov. The only other records of Cyclostomiceratinae from Baltoscandia are provided by de Verneuil (1845) and Mutvei and Stumbur (1971) who described *Pictetoceras eichwaldi* (de Verneuil, 1845) from the upper Kundan Stage of Estonia. The Swedish representatives of the family are slightly older.

HISTORICAL REVIEW OF THE FAMILY CYCLOSTOMICERATIDAE

Foerste (1925) originally proposed Cyclostomiceratinae for the genera *Cyclostomiceras* Hyatt, in Zittel, 1900 and *Eremoceras* Hyatt, 1884, believing that their siphuncle wall was characteristically holochoanitic, although no material was apparently sectioned to confirm this feature. Ulrich and Foerste (1936) added their new genus *Amphoroceras*, based upon *Cyclostomiceras minimum* (Whitfield, 1886). Later, Ulrich *et al.* (1943) regarded *Amphoroceras* as a junior synonym of *Cyclostomiceras* and added their new genera *Buehleoceras* and *Bridgeoceras* to the family. They also figured thin sections of the siphonal wall of *Cyclostomiceras* indicating that this genus actually possessed very short septal necks and thick, layered connecting rings. Ulrich *et al.* (1944) later added *Dresseroceras* to the Cyclostomiceratinae; the holotype of its type species, and the only known specimen of this monospecific genus, is represented by the internal mould of a body-chamber which bears prominent but irregularly spaced transverse annulations. The structure of the siphuncle wall remains unknown.

Cecioni (1953) described the new cyclostomiceratid *Paracyclostomiceras* from the Llanvirn of Serrania de Zapla, northern Argentina and illustrated the detail of the siphuncle wall. In their description of nautiloids from the lower Ordovician of Virginia, Unklesbay and Young (1956) included *Woosteroceras* Ulrich, Foerste, Miller and Unklesbay, 1944 within the Cyclostomiceratinae, and later Balashov (1962, p. 74, pl. 5, fig. 13) included *Pictetoceras* Foerste, 1926, demonstrating that the connecting rings of this latter genus were of thickened ellesmerocerid type.

Furnish and Glenister (1964) placed Cyclostomiceratinae in synonymy with Ellesmeroceratinae Kobayashi, 1934. This procedure united a large number of taxa with comparable siphuncular features: short achoanitic to orthochoanitic septal necks, thick-layered connecting rings and siphonal diaphragms (where known). However, the synonymy adopted by Furnish and Glenister (1964) also incorporated taxa exhibiting a wide variety of conch forms within the single family Ellesmeroceratinae and this approach is now regarded as obscuring a number of distinct lineages. The same authors regarded *Dresseroceras* as a synonym of the protozyclocleratid genus *Protozyclocleras* Hyatt, in Zittel, 1900, although the former genus also bears a strong morphological resemblance to other annulate protozyclocleratids such as *Catoraphiceras* Ulrich and Foerste, 1936 and *Walcottoceras* Ulrich and Foerste, 1936.

Flower (1964) recognized a varied series of morphotypes within the Ellesmeroceratinae ranging from orthocones and simple cyrtocoines to specialized forms with contracted or 'crested' apertures. He used these morphotypes for descriptive purposes but his morphogroups were not intended to represent independent lineages within the family. However, he acknowledged that the diversity of taxa then assigned to the Ellesmeroceratinae was unrealistic and re-introduced a number of previously used family names including Cyclostomiceratinae Foerste, 1925 for the genera *Cyclostomiceras*, *Paracyclostomiceras* and *Pictetoceras*. Mainly on the basis of conch form, he retained *Eremoceras*, *Buehleoceras* and *Woosteroceras* within a still highly diverse family Ellesmeroceratinae, and regarded *Bridgeoceras* as an ellesmerocerid of uncertain affinities. He also

regarded *Dresseroceras* as a synonym of *Bridgeoceras* which itself was an 'ellesmeroceroid of uncertain position'.

Mutvei and Stumbur (1971) provided a comprehensive study of *Pictetoceras* from the Llanvirn (Kundan; Aluojan Substage) of Estonia, and noted the presence of siphonal diaphragms and muscle-scar impressions in the type species *P. eichwaldi* (de Verneuil, 1845). Chen Jun-yuan (*in Qi et al.* 1983) described the new genus *Eocyclostomiceras* from the lower Ordovician of northern Jiangxi Province, east China, but assigned the taxon to the Ellesmeroceratidae. This latter genus is poorly known but available morphological and stratigraphical evidence tentatively supports assignment to the Cyclostomiceratidae.

Dzik (1984) recognized that the Ellesmeroceratidae contained a diverse range of conch forms and lineages, and introduced the family Oneotoceratidae for relatively short, compressed, endogastrically curved shells including *Buehleroceras*. He also distinguished the Cyclostomiceratidae as a small group of late Arenig to early Llanvirn inflated orthoconic nautiloids but synonymized both *Pictetoceras* and *Paracyclostomiceras* within *Cyclostomiceras*. For reasons described below, I regard these three genera as distinct.

ORIGIN OF THE FAMILY CYCLOSTOMICERATIDAE

Flower (1964, pp. 123–124) regarded the Cyclostomiceratidae as being derived from the ellesmerocerid family Baltoceratidae Kobayashi, 1935 during the late Canadian (Cassinian). He noted, in particular, that the Cassinian genus *Metabaltoceras* Flower, 1964 was intermediate between the two families in its overall form but departed from the generalized pattern in its relatively large ventral siphuncle and sutural lobes. The fusiform shell and achoanitic septal necks in *Metabaltoceras* offer some support for this possible relationship.

The conch cross section of taxa assigned to the Cyclostomiceratidae is usually sub-circular to compressed, and is more reminiscent of the Bassleroceratidae than the Baltoceratidae in which it tends to be slightly depressed. Bassleroceratidae had a widespread distribution in the mid to late Canadian and several genera (*Avaoceras*, *Diaphoroceras* and *Lawrenceoceras* Ulrich, Foerste, Miller and Unklesbay, 1944) show features reminiscent of the Cyclostomiceratidae, namely contraction of the body-chamber near the aperture and very short septal necks with thick connecting rings (Flower 1964, p. 152; Furnish and Glenister 1964, p. K 148). However, the Bassleroceratidae are represented mainly by longicones and consequently, despite superficial similarities, an origin for the Cyclostomiceratidae from a bassleroceratid ancestor is thought to be unlikely.

Cyclostomiceratids also bear a close external resemblance to some bathmoceratid genera described from the upper Canadian of Argentina and Bolivia by Cecioni and Flower (1985). Bathmoceratidae is a group of ellesmerocerid nautiloids characterized by inflated and greatly thickened connecting rings which project adorally or laterally towards the siphuncle; these connecting rings are commonly associated with numerous diaphragms. However, the structure of the bathmoceratid siphuncle wall is wholly unlike siphonal features known within the Cyclostomiceratidae. In addition, the body-chambers belonging to the bathmoceratids described by Cecioni and Flower (1985) do not appear to contract adorad which is a characteristic feature of cyclostomiceratid taxa. Consequently, there appears to be no clear evidence to link the origins of the Cyclostomiceratidae and the Bathmoceratidae, and any similarity in external conch form is regarded here to be essentially homeomorphy.

A possible origin for the Cyclostomiceratidae from within the Oneotoceratidae (Dzik 1984) does, however, require serious consideration. Dzik's (1984) interpretation of the latter family included stout breviconic or near-gomphoceroid endogastric forms in addition to distinctive, strongly cyrtoconic brevicones. The oneotoceratids appear to exhibit very short septal necks with thickened, layered connecting rings which are highly comparable to those of the Cyclostomiceratidae, although the former family generally possesses a slightly narrower siphuncle. Further evidence for deriving the Cyclostomiceratidae from the Oneotoceratidae is provided here by *Microstomiceras* gen. nov. which indicates that the former family may also be endogastric.

Current evidence would therefore indicate that the Cyclostomiceratidae developed in the late Canadian (Cassinian) from either the Baltoceratidae (via *Metabaltoceras*) or more likely from gomphoceroïd-breviconic forms assigned to the Oneotoceratidae.

SYSTEMATIC PALAEOONTOLOGY

The terminology used here follows that of Flower (1964) and Furnish and Glenister (1964). The type material of newly described species is held in collections at the Swedish Museum of Natural History (Naturhistoriska Riksmuseet, RM), Stockholm and the Swedish Geological Survey (Sveriges Geologiska Undersökning, SGU), Uppsala.

Class CEPHALOPODA Cuvier, 1797

Order ELLESMEROCERIDA Flower, *in* Flower and Kummel, 1950

Family CYCLOSTOMICERATIDAE Foerste, 1925

Diagnosis. Gomphoceroïd to vasiform brevicones, shell straight or with faint endogastric or exogastric curvature. Conch section sub-circular to slightly compressed or depressed, rapidly expanding over the phragmocone; aperture typically contracted but never markedly constricted. Sutures transverse or with dorsal and ventral saddles and corresponding lateral lobes. Siphuncle (sub)ventral, with achoanitic to suborthochoanitic or orthochoanitic septal necks; segments concave and outlined by thick, layered connecting rings. Siphonal diaphragms known in some genera.

Remarks. Conch form within the Cyclostomiceratidae varies: *Cyclostomiceras* and *Paracyclostomiceras* are essentially straight brevicones (Ulrich *et al.* 1943, pls 31–34; Cecioni 1953, pl. 3) whilst *Microstomiceras* gen. nov. is clearly endogastric. Mutvei and Stumbar's (1971) reconstruction of *Pictoceras eichwaldi* (de Verneuil, 1945) proposes a straight, breviconic shell with a very large protoconch, although available evidence (based on *Cyclostomiceras cassinense* and *C. depressum* in Ulrich *et al.* 1943 and *Microstomiceras hohni* gen. et sp. nov.) indicates that the protoconch of cyclostomiceratids was, in fact, relatively small. This is consistent with Dzik's (1984, p. 22) suggestion that the apical parts of ellesmerocerids may represent nautiloids with a small planktonic larval stage.

Genera assigned. Cyclostomiceratidae is regarded here as a distinct family of breviconic ellesmerocerids containing the following taxa: *Cyclostomiceras* Hyatt, *in* Zittel, 1900; *Pictoceras* Foerste, 1926; *Paracyclostomiceras* Cecioni, 1953; *Eocyclostomiceras* Chen, *in* Qi *et al.*, 1983 and *Microstomiceras* gen. nov.

Occurrence. Arenig (upper Canadian, Cassinian) to lower Llanvirn of the USA, Baltoscandia, northern Argentina and east China.

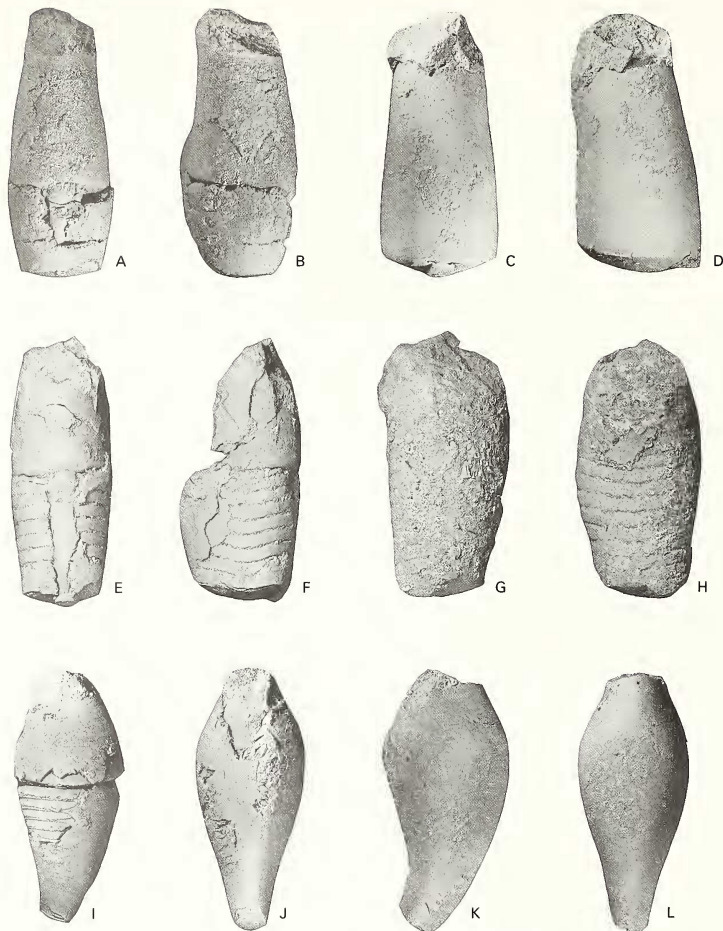
Genus CYCLOSTOMICERAS Hyatt, *in* Zittel, 1900

(= *Amphoroceras* Ulrich and Foerste, 1936)

Type species. *Gomphoceras cassinense* Whitfield, 1886; by original designation (Hyatt, *in* Zittel 1900, p. 611).

Diagnosis. Gomphoceroïd, breviconic orthocones with circular to depressed section; phragmocone expanding forward fairly rapidly, anterior half of mature body-chamber slightly contracted. Sutures and growth lines straight and directly transverse. Siphuncle small, about 15 per cent. of conch diameter, ventral in position but not marginal. Septal necks orthochoanitic, connecting rings thick and layered.

Remarks. Apart from the type species *C. cassinense* (Whitfield), the following taxa are also assigned to the genus: *C. minimum* (Whitfield, 1886), *C. depressum* Ulrich, Foerste and Miller, 1943 and



TEXT-FIG. 3. A-D, *Pictoceras oliviae* sp. nov.; lower Hølen Limestone Formation, Hølludden, northern Öland. A-B, ventral and left lateral views of holotype, RM Mo158460a; $\times 1.75$. C-D, ventral and left lateral views of paratype, RM Mo158441; $\times 2.7$. E-H, *Paracyclostomiceras paucitumidum* sp. nov.; lower Hølen Limestone Formation, northern Öland. E-F, ventral and left lateral views of holotype, SGU Ce001, from Enerum; $\times 1.25$. G-H, ventral and left lateral views of paratype, SGU Ce002, from Hølludden; $\times 1.75$. I-L, *Microstomiceras holmi* gen. et sp. nov.; lower Hølen Limestone Formation, Hølludden, northern Öland. I, right lateral view of holotype, RM Mo158700; $\times 3.3$. J-L, ventral, right lateral and dorsal views of paratype, RM Mo158698; $\times 3.75$.

C. depressius Cecioni, 1953. *Cyclostomiceras? vasiforme* (Dwight, 1884) is of uncertain status; according to Flower (1964, p. 124), the weathered section of a *Bassleroceras* would produce a form analogous to the type specimen. The expansion rate and conch form of the specimen tends to confirm that its assignment to the Cyclostomiceratidae is incorrect.

Occurrence. Cecioni (1953) reported *C. depressius* from the Arenig of Quebrada de Coquena, Purmamarca, Chile; *C.? vasiforme* is recorded from the Mid Canadian Rochdale Limestone of southern New York. All the remaining taxa occur in the Fort Cassin Limestone of the Champlain Valley, Addison County, Vermont or the Smithville Formation of Lawrence County, Arkansas (both occurrences are of Arenig age).

Genus PICTETOCERAS Foerste, 1926

Type species. *Gomphoceras eichwaldi* de Verneuil, 1845, p. 357; by original designation (Foerste 1926, p. 327).

Diagnosis. Conch gomphoceroid, enlarging as far as anterior part of the phragmocone then contracting adorally. Shell section compressed; sutures inclined forward over the venter. External conch surface ornamented with weak, indistinct growth lines. Body-chamber relatively long, apertural margin with a distinct, unpaired dorsal sinus and weaker ventral sinus; camerae narrow, 10–15 per cent. of the dorso-ventral diameter. Siphuncle circular in section, in contact with ventral wall, 20–25 per cent. of conch diameter. Septal necks orthochoanitic; connecting rings three to four times thicker than septa and layered. Apical portions of siphuncle traversed by numerous, adorally arching calcareous diaphragms.

Remarks. *Pictetoceras* was reviewed by Mutvei and Stumber (1971) who regarded the genus as monospecific and described the type species, *P. eichwaldi*, from the upper Kundan Stage (Aluojan Substage) of the St Petersburg district and Estonia. A slightly older species, *P. oliviae* sp. nov., is described here from the lower Kundan of Öland. This new species is much smaller than *P. eichwaldi* (based on the assumption that contraction of the aperture with septal approximation is indicative of maturity in individual specimens). The type material of *P. oliviae* sp. nov. does not exhibit siphonal diaphragms, although it is likely that no material sufficiently apical to contain such structures has been sectioned.

Occurrence. Kundan Stage (uppermost Arenig to lower Llanvirn) of Öland, Sweden, Estonia and the St Petersburg district.

Pictetoceras oliviae sp. nov.

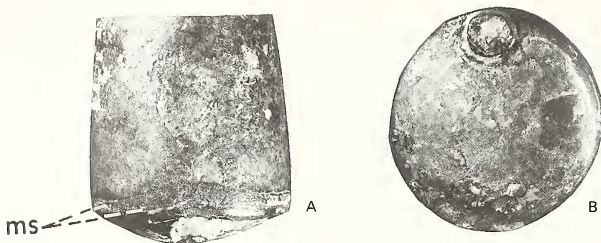
Text-figures 3A–D, 4, 6A

Derivation of name. For Olivia Holm, the daughter of Gerhard Holm, who collected the holotype specimen in 1896.

Material. The holotype (RM Mo158460a) is an unsectioned conch with a complete body-chamber and several adoral camerae. Three paratypes (Mo158441, 158457, 158460b–d) consist of incomplete sectioned phragmocones and/or body-chambers. All the type material was collected by Olivia and Gerhard Holm in 1890 and 1896, from the lower Holen Limestone Formation (lower Kundan Stage) at Hälludden, northern Öland.

Diagnosis. Small, slender *Pictetoceras* with sub-circular section and elongate body-chamber which gradually contracts adrad.

Description. Conch small and slender, vasiform-breviconic with sub-circular section. Holotype is most complete specimen examined; length 24.2 mm, adoral 14.2 mm representing body-chamber. Latter relatively long (estimated 40 per cent. of total conch length) and contracting slowly towards aperture; contraction



TEXT-FIG. 4. *Pictetoceras oliviae* sp. nov.; RM Mo158441, paratype; lower Hølen Limestone Formation Hälludden, northern Öland. A, ventral view of base of body-chamber showing annular retractor muscle scar (ms) with indistinct lobes concentrated ventrally; $\times 4.6$. B, shell cross section, venter and siphuncle uppermost; $\times 5$.

greater on ventral side, dorsal side only slightly concave. External shell surface smooth with very faint growth lines which trace out feeble dorsal and ventral sinuses. Maximum conch width in holotype near top of phragmocone where dorsoventral diameter is 12.4 mm; at apical end, dorso-ventral diameter is 10.3 mm with lateral width 9.4 mm. Body-chamber bears faint muscle-scars consisting of annular retractor scar with indistinct lobes concentrated ventrally (Text-fig. 4A). Sutures laterally transverse, becoming very weakly inclined over venter and dorsum. Average cameral height 1.1 mm, septal concavity shallow. At base of body-chamber, siphuncle represents 26 per cent. of conch diameter, reducing to 15 per cent. at apical end. Septal necks orthochoanitic, extending apicad 0.2 camerae. Connecting rings thick and layered; inner layer (adjacent to siphuncle) dark and comparable in thickness to septa, outer layer (adjacent to camerae) paler and three to four times septal thickness (Text-fig. 6A).

Remarks. *P. oliviae* sp. nov. differs from the type species, *P. eichwaldi*, in its smaller size and relatively long body-chamber. The ventromyarian muscle scars observed at the base of the body-chamber in *P. oliviae* sp. nov. are similar in form to those described for the type species of *Pictetoceras* by Mutvei and Stumbur (1971, p. 120).

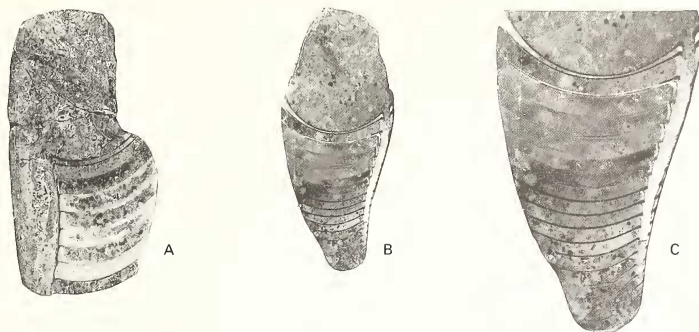
Occurrence. The species is known only from the lower Hølen Limestone Formation (lower Kundan Stage) at Hälludden, northern Öland. The specimens collected in the last century were obtained from either the Hunderumian or Valasteian substages, or both. Several other specimens collected recently from Hälludden are also likely to belong to this species but require further study to confirm this assignment. These specimens come from the lowermost part of the Valasteian Substage (Jaanusson and Mutvei 1982, p. 16), between 0–0.05 m and 0–15 m below the main discontinuity surface.

GENUS PARACYCLOSTOMICERAS Cecioni, 1953

Types species. *Paracyclostomiceras floweri* Cecioni, 1953; by original designation (Cecioni 1953, p. 98).

Diagnosis. Similar to *Cyclostomiceras* but sutures undulatory with well-developed dorsal and ventral saddles and corresponding lateral lobes.

Remarks. This genus is similar in overall conch form to *Cyclostomiceras* but is readily identified by the form of its sutures. Cecioni (1953) noted that the apertural contraction rate of *Paracyclostomiceras* was smaller than that known for *Cyclostomiceras*, and that the siphuncle was in contact with the ventral wall of the conch (according to Cecioni, the siphuncle is slightly removed from the venter in *Cyclostomiceras*). Apart from the type species, he also described *P. depressum*



TEXT-FIG. 5. Polished dorso-ventral sections of conchs, all from the lower Holen Limestone Formation of northern Öland. A, *Paracylostomiceras paucitimidum* sp. nov.; SGU Ce001, holotype; Enerum. B-C, *Microstomiceras holmi* gen. et sp. nov.; RM Mo158700, holotype; Hälludden. B, $\times 3.75$. C, detail of same; $\times 7$.

which (as its name implies) has a more depressed conch section than *P. floweri*. The Swedish species, *P. paucitimidum* sp. nov., has a less inflated conch form and is distinctly compressed in section.

Occurrence. The genus has been recorded only from the Llanvirn of Argentina and Sweden. The South American specimens were collected from Rio Las Capillas and Garrapatal, Serrania de Zapla, northern Argentina from a horizon with *Hoekaspis schlagintweiti* Harrington and Leanza. Associated trilobite (*Hoekaspis-Famatinolithus*) and graptolite (*Didymograptus bifidus*-*D. climacograptoides* group) faunas support an early Llanvirn age (Aceñolaza 1976). *P. paucitimidum* sp. nov. is known from the lower Kundan Stage (uppermost Arenig or lower Llanvirn) of northern Öland.

Paracylostomiceras paucitimidum sp. nov.

Text-figures 3E-H, 5A, 6B

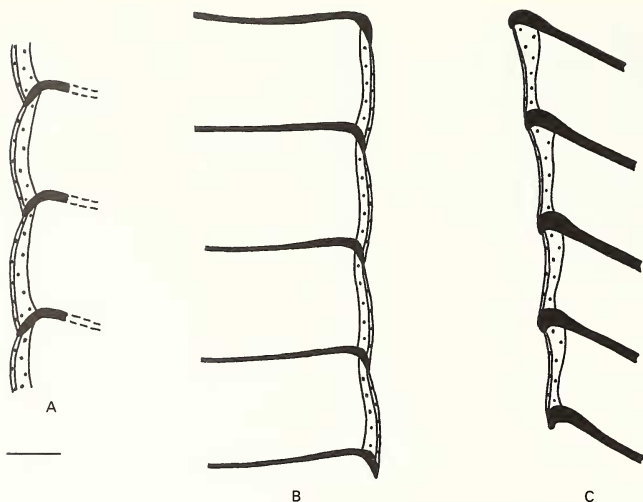
Derivation of name. From Latin *paucus* meaning little and *timidus* meaning swollen, referring to the relatively slender conch form of this species.

Material. The holotype (SGU Ce001) and paratype (SGU Ce002) consist of incomplete dorso-ventrally sectioned phragmocones with portions of the body-chamber remaining. Both specimens were collected by Gerhard Holm in 1895 from the lower Holen Limestone Formation (lower Kundan Stage) of northern Öland; the holotype is from Enerum, the paratype from Hälludden.

Diagnosis. Relatively slender *Paracylostomiceras* with compressed section.

Description. Conch slender, vasisform-breviconic with conspicuously compressed section. Body-chamber in both holotype and paratype incomplete but gradually contracting adoral.

Holotype 41.9 mm long, adoral 20.5 mm representing body-chamber. Remainder of phragmocone consisting of nine camerae, each *c.* 2.0 mm high except for adoral camerae where septa approximated and 0.7 mm apart. Lateral compression of conch evident at apical end where dorso-ventral diameter 14.9 mm and lateral width 12.1 mm. Sutures undulatory, forming broad and conspicuous apically directed lobes; septa shallowly concave. Siphuncle ventral, sub-circular, 25 per cent. of conch diameter. Septal ridges distinct, comprising sharp, adorally directed raised lines 2.2 mm apart on venter. Septal necks orthochoanitic, extending apicad 0.25 to 0.3 camerae. Connecting rings thick and layered (Text-fig. 6B), with inner dark layer (adjacent to siphuncle) and



TEXT-FIG. 6. *Camera lucida* drawings of the structure of the siphuncle wall; solid shading indicates septa, stippling represents layered connecting rings. A, *Pictetoceras oliviae* sp. nov.; RM Mo158460b, paratype. B, *Paracyclostomiceras paucitumidum* sp. nov.; SGU Ce001, holotype. C, *Microstomiceras holmi* gen. et sp. nov.; RM Mo158700, holotype. Scale bar represents 0.5 mm (A), 1 mm (B) and 0.25 mm (C).

outer, paler thicker layer (adjacent to camerae). Fragments of external shell confirm conch surface to be virtually smooth with inconspicuous feeble growth lines.

Paratype similar to holotype but smaller; 31.4 mm long, adoral 12.7 mm representing body-chamber; remaining 18.7 mm of phragmocone consisting of ten camerae varying in height from 1.5 mm to 1.9 mm.

Remarks. *Paracyclostomiceras paucitumidum* sp. nov. is readily distinguished from other species assigned to the genus by its laterally compressed conch section.

Occurrence. Lower Hølen Limestone Formation (lower Kundan Stage; Hunderumian and/or Valasteian substages) of Enerum and Hälludden, northern Öland.

Genus EOCYCLOSTOMICERAS Chen, in Qi *et al.*, 1983

Type species. *Eocyclostomiceras ventrum* Chen, in Qi *et al.* 1983; by original designation (Chen, in Qi *et al.*, 1983, p. 305).

Remarks. *Eocyclostomiceras* is a poorly known genus described from incomplete, sectioned (but apparently gomphoceroid) phragmocones with the apical portion of a body-chamber preserved in the holotype of the type species. The siphuncle is relatively narrow, accounting for c. 10–15 per cent. of the conch diameter; septal necks short, probably orthochoanitic, connecting rings thick and layered. The sub-circular shell section and structure of the siphuncle wall tentatively support assignment of the genus to the Cyclostomiceratinae, although the overall conch form is unknown

and more detailed comparison with other genera is not possible. Further study may prove the genus to be synonymous with *Cyclostomiceras*. Apart from the type species, Chen Jun-yuan (*in Qi et al.* 1983) also described *E. subventrum* (with subventral siphuncle) and *E. clinoseptatum* (with steeply inclined septa).

Occurrence. All three species of *Eocyclostomiceras* are reported from the lower Ordovician (Dawan Formation or equivalent) of northern Jiangxi Province, east China. Associated cephalopods, including *Hemichoanella canningi* Teichert and Glenister, indicated a late Canadian (Arenig) age.

Genus MICROSTOMICERAS gen. nov.

Type species. *Microstomiceras holmi* sp. nov.

Derivation of name. From Greek *mikro* meaning little and *stoma* meaning mouth, referring to the small, contracted aperture of this taxon and its small conch size.

Diagnosis. Very small, slightly endogastric gomphoceroid brevicone with moderate expansion rate enlarging to base of body-chamber and then contracting adorally; body-chamber 30–35 per cent. of total length. Shell surface ornamented with weak, indistinct growth lines. Conch section sub-circular to slightly compressed, sutures nearly transverse with faint inclination forward over dorsum. Camerae narrow, comprising 9 per cent. of dorsoventral diameter, siphuncle slightly removed from ventral shell wall, representing approximately 10 per cent. of conch width adorally increasing to 18 per cent. apically. Septal necks very short, suborthochoanitic to achoanitic; connecting rings thick and layered.

Remarks. This monospecific genus is readily distinguished from all other cyclostomiceratids by its small size and slight endogastric curvature. *Microstomiceras* gen. nov. is one of the smallest nautiloids yet described from the Lower Palaeozoic.

Occurrence. Lower Kundan Stage (uppermost Arenig to lower Llanvirn) of northern Öland, Sweden.

Microstomiceras holmi sp. nov.

Text-figures 3I–L, 5B–C, 6C

Derivation of name. In honour of the eminent Swedish palaeontologist Gerhard Holm (1853–1926) who collected the type material.

Material. The holotype (RM Mo158700) is a nearly complete specimen which has been dorso-ventrally sectioned. Three paratypes are also designated: Mo158697 is a thin section through a portion of a phragmocone and body-chamber; paratypes Mo158698–158699 are sub-complete, unsectioned phragmocones with body-chamber. None of these specimens retain the apicadmost tip of the conch. All the material was collected by Gerhard Holm (in 1895 and 1909) from the 'grey vaginatum limestone' (lower Holen Limestone Formation) at Hälludden, northern Öland.

Description. Very small, slightly endogastric gomphoceroid brevicones less than 14 mm long. Holotype 11.5 mm long with maximum width 5.5 mm; body-chamber 3.9 mm long, approximately 34 per cent. of total conch length. Conch expansion rate moderate, maximum width attained at base of body-chamber. Body-chamber contracts adorally by similar amounts on dorsal and ventral sides, aperture 55–60 per cent. of maximum conch width. Conch section sub-circular, becoming slightly compressed apically. Shell surface smooth, ornamented with indistinct growth lines only. Sutures nearly transverse with slight adorally directed, broad saddle over dorsum. Siphuncle slightly removed from venter, nearly 10 per cent. of conch diameter adoral and 18 per cent. apicad. Septa shallow, average cameral height 0.5 mm; in holotype, last-formed septum approximated. Septal necks very short, achoanitic to suborthochoanitic; connecting rings thick and layered but tapering and

thinning slightly in apical region of camerae (Text-fig. 6C). Diaphragms not visible but apicadmost tips lacking from all conchs examined.

Remarks. No specimens of *Microstomiceras holmi* sp. nov. examined exceed 14 mm in total length; this figure allows for the apicadmost tips of the conchs which are missing. The adoral contraction of the body-chamber and approximation of the last-secreted septa are regarded here as being reliable indicators of maturity. Consequently *M. holmi* sp. nov. is the smallest cyclostomiceratid known and the first member of the family known to possess a definite endogastric shell.

Occurrence. Lower Hølen Limestone Formation (lower Kundan Stage, Hunderumian to lower Valastean substages) at Hälludden, northern Öland.

CONCLUSIONS

Cyclostomiceratidae is a family of short breviconic to gomphoceroid nautiloids recorded from the Arenig and Llanvirn (lower Ordovician) of the USA, Baltoscandia, northern Argentina and east China (Jiangxi Province). It is distinguished from all other ellesmerocerids by its combination of shell form, with contracted apertures and achoanitic to orthochoanitic septal necks outlined by thick connecting rings.

As is common with many other Lower Palaeozoic nautiloids, the new Swedish taxa described in this paper are based on only a few specimens. Current knowledge indicates that although Cyclostomiceratidae possessed a wide palaeogeographical range, they were not common elements of early Ordovician nautiloid faunas. Consequently, it is not possible on present evidence to gauge the amount of intraspecific variation that these nautiloids may exhibit. However, the combination of distinct morphological features, excellent preservation and stratigraphical position, provides ample evidence for regarding the cyclostomiceratids from Öland as representing new and distinct taxa. In particular, *Microstomiceras* gen. nov. is one of the smallest nautiloids yet described from the Lower Palaeozoic.

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